Aspects of the Biology of *Donax gouldi*
And a Note on Evolution in Tellinacea (Bivalvia)

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(5 Text figures)

INTRODUCTION

Donax gouldi DALL, 1921, is a small bivalve that lives in the surf zone of sandy marine beaches and ranges from Santa Barbara, California, to Acapulco, Mexico. Although the Tellinacea are generally regarded as nonselective deposit feeding organisms, *D. gouldi* feeds in a different manner to be described below.

MORI (1938, 1950), HEDGPETH (1953), TURNER & BELDING (1957), LOESCH (1957), and WADE (1964) have shown that various species of *Donax* maintain their position in the surf zone by horizontal migration with the tide. The adaptations that permit *D. gouldi* to occupy this zone are discussed.

MORPHOLOGY

Shell: As shown in Figure 1 the thick shell of *Donax gouldi* is elongate, being almost twice as long as it is high. This shape is highly adaptive for burrowing movements with the anterior end undermost, as shown for species of *Solen* and *Siliqua* (POHLO, 1963). Most specimens are about 1.5 cm long but can be as large as 2.5 cm.

Mantle Cavity: The organs of the mantle cavity are shown in Figure 1. It is seen that the ctenidia (C) are large and the labial palps (LP) small. In many of the Tellinacea the outer demibranch is upturned but this is not the case in *Donax gouldi* in which both demibranchs are complete.

Animals opened in the field had very little sand in the mantle cavity. If sand was present it was usually located at the site of pseudo-feces accumulation or on the foot but rarely on the ctenidia or labial palps. A mantle fold, on the anterior margin of the inhalant siphon in some other Tellinacea, is lacking.

Figures 1 and 3 show the feeding current pattern on the ctenidia and labial palps. The anatomical relationship of ctenidia and labial palps is of Category III (i. e., the anterior filaments of the inner demibranch are not inserted into a distal oral groove – STASEK, 1963). Material moves rapidly on the outer to the inner demibranch. Some material is carried toward the labial palps along the ventral margins of the outer demibranch but the current is weak and a food groove is absent. Material also goes under the outer demibranch (OD), and then moves dorsally. This same type of movement was observed by YONGE (1949, p. 59, fig. 22 b). There is a well-defined food groove on the inner demibranch (ID), and material is carried in it toward the labial palps. Most of the larger material is rapidly moved by ciliary activity perpendicular to the long axis of the palp folds (Figure 3).

Pedal Musculature: The pedal musculature (Figure 1) is more complex than is usually found within the Tellinacea. Here the anterior protractor muscle (AP) is split into three bands at the site of its insertion near the anterior adductor. An elevator pedis muscle (EP) is present, as is a small muscle, here termed the demibranch muscle (DM).

Siphons: The inhalant siphon (Figure 2) is ringed with six lobes. These lobes, which are pointed, have many frilly projections emanating from their sides and act as a straining device. The end of the siphon is shown expanded in Figure 2, but in life, the tentacles are usually very close together with little space between the interdigitating frills.

Observations were made on animals kept in a finger bowl half filled with sand. The inhalant siphon was seen to move up and down continually while it pushed aside sand grains. At all times the tentacles on the inhalant siphon were drawn close together and were actively rejecting sand grains. This is in contrast to *Donax vittatus* DA COSTA, where the siphonal tentacles are turned back and the siphons have no sieving action (YONGE, 1949).
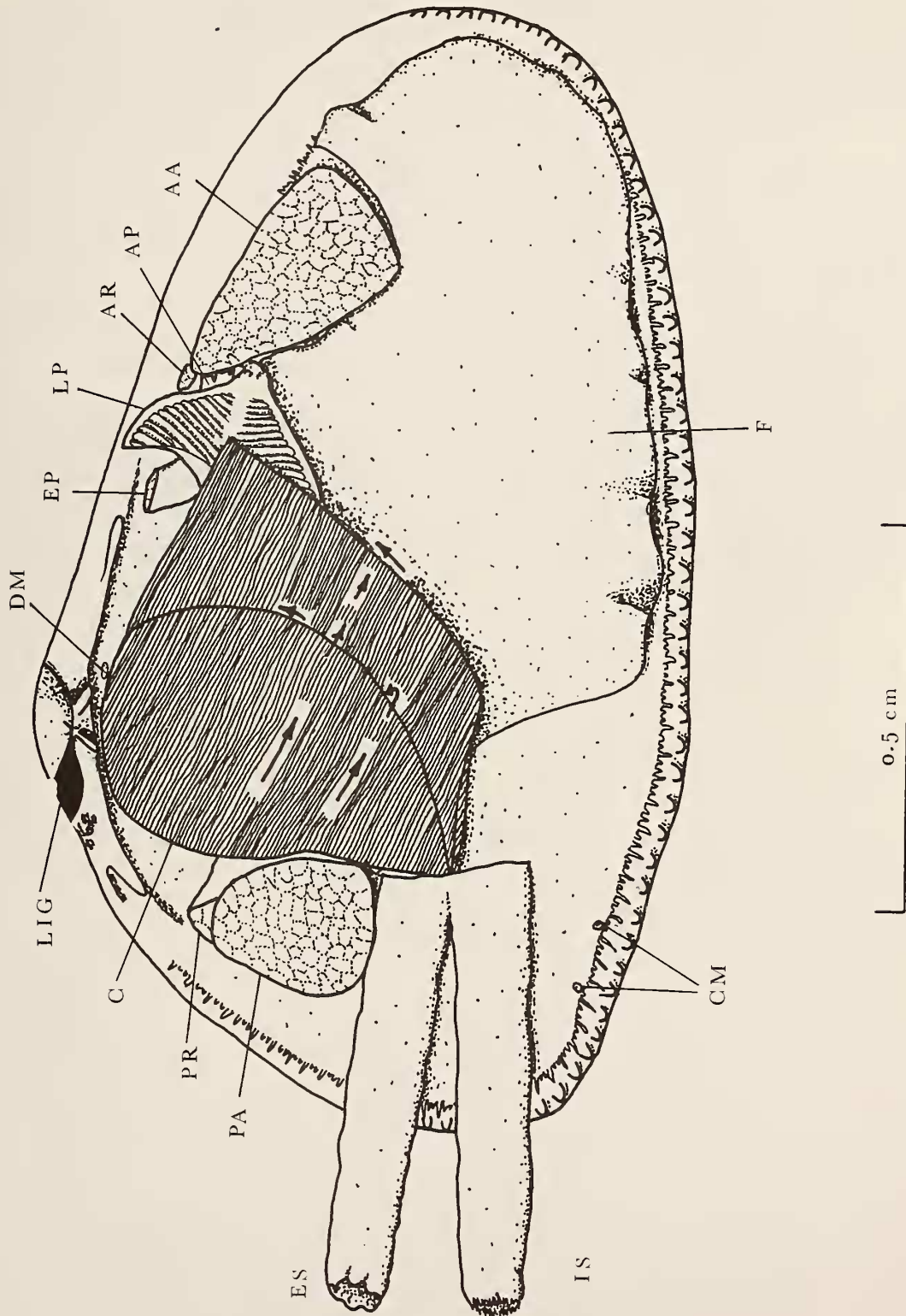
Figure 1

Donax gouldi. Mantle Cavity Viewed from the Right Side.

AA - anterior adductor; AP - anterior protractor; AR - anterior retractor; C - ctenidia; CM cruciform muscle; DM - demibranch muscle; EP - elevator pedis muscle; ES - exhalant siphon; F - foot; IS - inhalant siphon; LIG - ligament; LP - labial palp; PA - posterior adductor; PR - posterior retractor.

The exhalant siphon (ES) of *D. gouldi* terminates in six blunt lobes.

Stomach: The terminology used to describe the stomach is that of PURCHON (1957, 1958, 1960).

0.5 mm

Figure 2

Sieving Mechanisms on the Inhalant Siphon.

The stomach (Figure 4) is of Type IV (characterized by the major typhlosoles not entering any ducts from the digestive diverticulum on the anterior or right side of the stomach). Externally it has a large dorsal hood (DH) and a small postero-dorsal appendix (A). A left caecum (LC) is present and the major typhlosole (TY) leads into it, material being carried on the typhlosole into the caecum.

Rejected material moves on the inner side of the major typhlosole toward the mid gut (MG). The typhlosole thus extends from the left caecum to the intestine. The typhlosole does not enter the digestive diverticulum duct (DDD) as it does in the other Tellinacea (PURCHON, 1960). A large left pouch (LP) is present with its sorting areas (SA), and it has seven openings to the digestive diverticulum. The intestine is separate from the style sac (SS) which is not the situation in most of the Tellinacea studied by PURCHON (1960). There are some differences between *Donax gouldi* and *D. faba* GMELIN (described by PURCHON, 1960). The left caecum (LC) of *D. gouldi* receives seven ducts from the digestive diverticulum, whereas in *D. faba* there are only four. The appendix is much smaller in *D. gouldi*, and there is no sorting area no. 3 (see PURCHON, 1960, fig. 2).

The stomach contents of *Donax gouldi* were mainly green fragmented plant material, diatoms and some small sand grains. This is in contrast to *Macoma secta* which also lives in a sand substratum. In this species, the stomach is densely packed with relatively large sand grains.

MOVEMENT AND MAINTENANCE OF POSITION IN THE SURF ZONE

MORI (1938, 1960), HEDGPETH (1953), TURNER & BELDING (1957), LOESCH (1957) and WADE (1964) have described how various species of *Donax* migrate with the rise and fall of the tide. These authors concluded that the clams emerge from the sand when triggered by acoustic shocks made by the breaking waves. The bivalves are then carried up or down the beach by the wave swash, and in this manner they maintain their position in the wave and swash zone.

Donax gouldi does not migrate with the rise and fall of the tide but stays in one position on the beach. This is in opposition to a study done by JOHNSON (1966) where she found that *D. gouldi* exhibits the migration tendency, but to a lesser degree, as found in *D. fossor* SAY, 1823, *D. semigranosus* DUNKER, 1877 and *D. variabilis* PHILIPPI, 1847. The absence of migration was seen by noting the behavior of this organism at San Diego and Los Angeles, California, and at Estero Beach, Mexico, where a very dense population was studied. At the Mexico locale the animals were so densely packed that many were protruding half out of the sand due to the lack of digging space. A similar population was reported at La Jolla, California, by COE (1953). These exposed animals made it easy to gauge the gross extent of the aggregation. They occurred in a band about 10 m wide at a tidal height of about one-half a foot below mean lower low water. When encountered on a minus tide at Estero Beach, the main population was completely separated from the swash zone by a distance of 15 m. This was taken as evidence that the animals do not maintain a position in the swash zone by migration.

Whereas migrating *Donax* pop out of the sand when a shock goes through the substratum, *D. gouldi* digs farther into the soil. This was seen by taking 33 specimens and placing them in a water and sand filled bucket. One
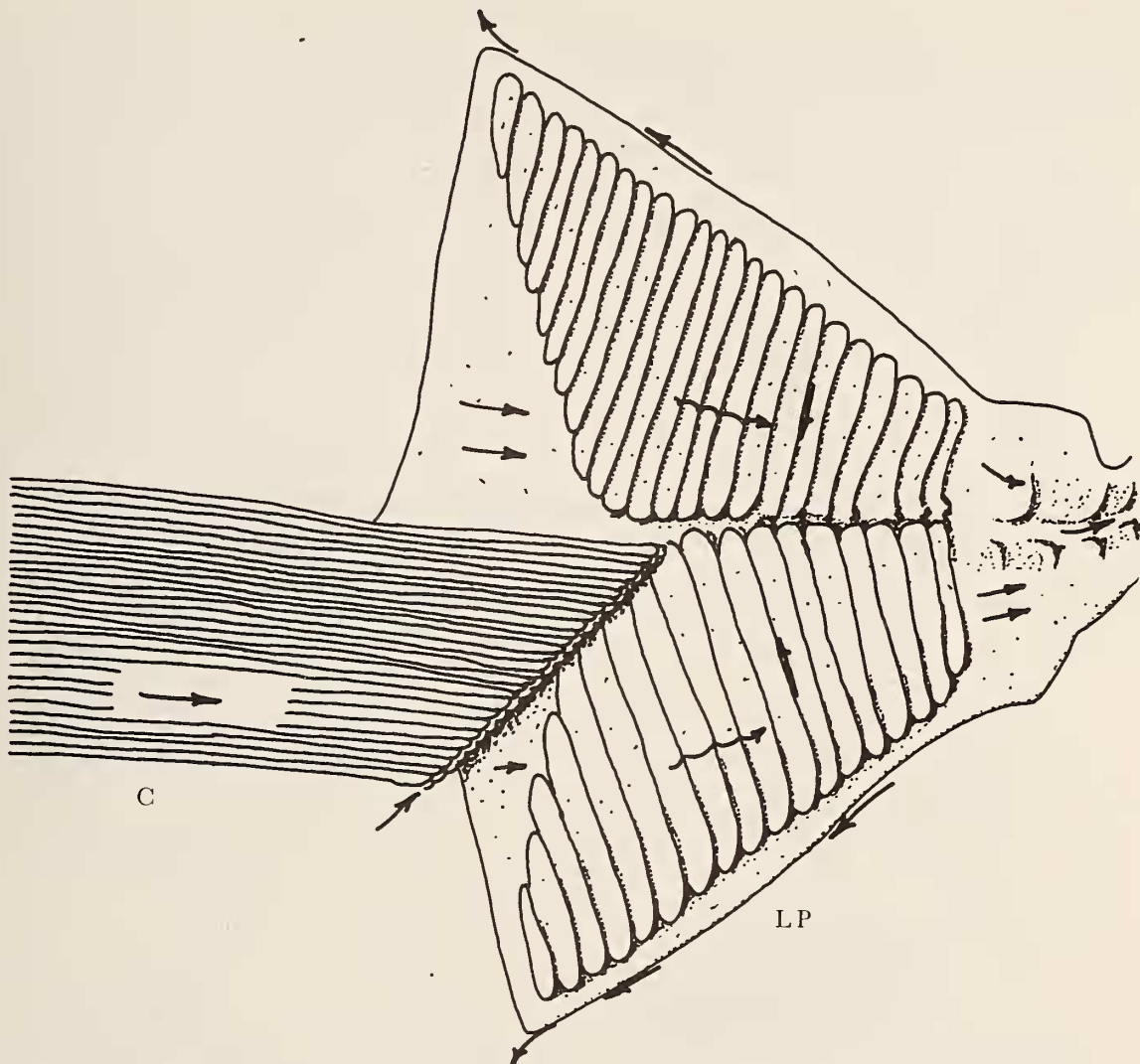
Figure 3

Feeding Currents on the Labial Palps (LP).
Most of the material is carried on the current perpendicular to the
long axis of the palp folds. G - gills.

animal began to burrow immediately, but the remainder did not burrow until the side of the bucket was pounded. After agitating the bucket, all but 10 burrowed into the sand. The most effective stimulus for burrowing seemed to be a combination of agitating the animal and rolling it about in a stream of water, conditions which occur naturally in the surf zone.

On the beach, when *Donax gouldi* happens to be unearthed by waves they extend their siphons and foot and these act as a drag preventing the animal from being carried the full advance of the swash. The foot, particularly, does an effective job of acting as a drag. Jacobson (1955) has described a similar behavior in *D. fossor*. In *D. gouldi*, as soon as the individual wave has subsided enough, the unearthed animal begins to flatten the foot against the substratum and then insert it into the sand as the siphons are being withdrawn. The animal then rapidly
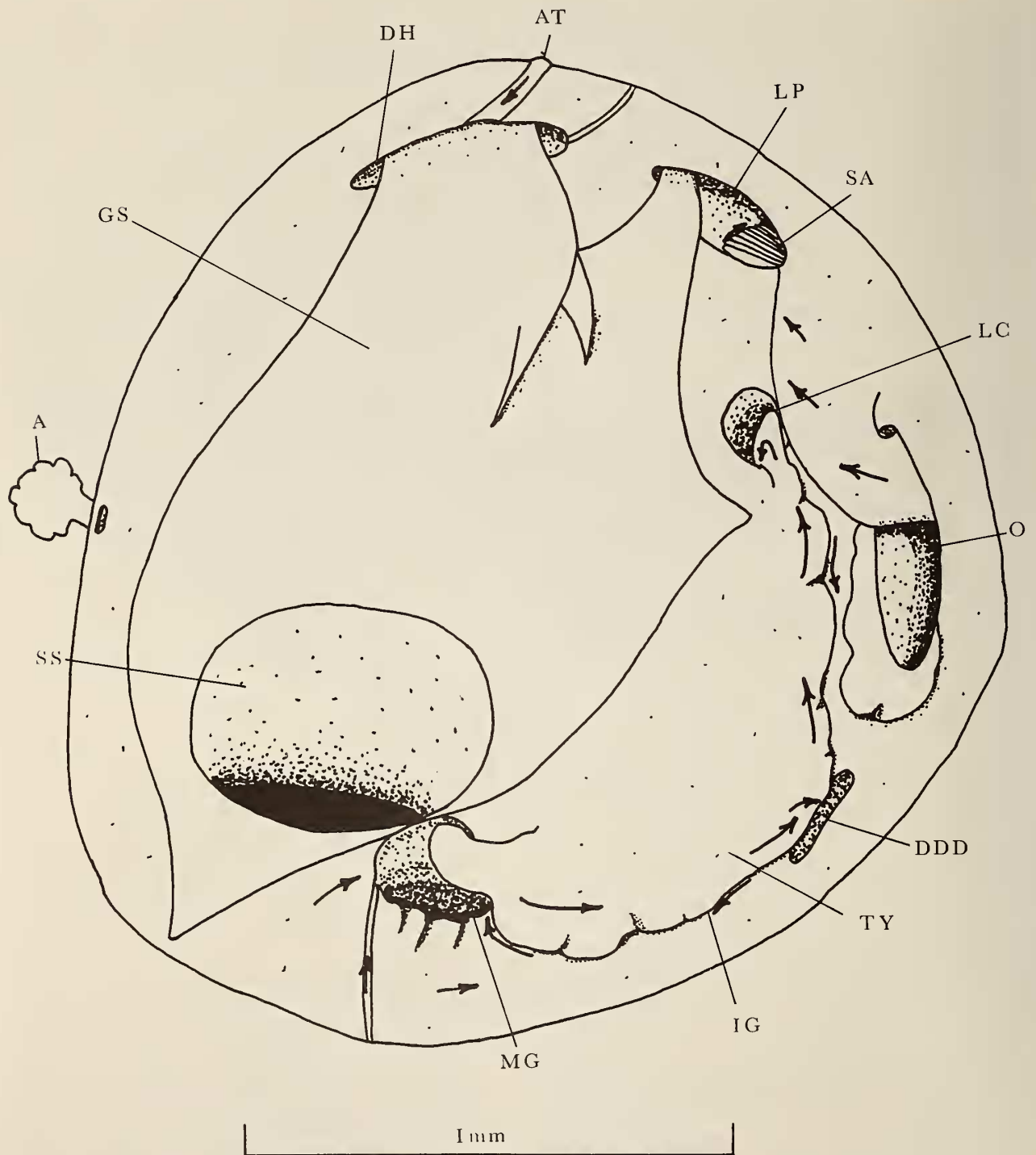
Figure 4

The Stomach of *Donax gouldi* after Dissection from the Dorsal Side.

A - appendix; AT - acceptance tract; DDD - digestive diverticular duct; DH - dorsal hood; GS - gastric shield; IG - intestinal groove; LC - left caecum; LP - left pouch; MG - mid gut; O - oesophagus; SA - sorting areas; SS - style sac; TY - major typhlosole.

rocks back and forth and is buried by a combination of its digging movements and a scouring of the sand, which is described by Johnson (1957).

To obtain an estimate of the density of the population at Estero Beach, random samples were taken within the 10 meter wide band. A metal frame 10 cm on a side was inserted to a depth of 1 cm and then a metal plate was inserted under the frame. Twenty samples were taken and the number of animals per quadrant ranged from 162 to 521. The average was 322.1 ± 18.76 animals per $100 \, cm^2$ of surface area. This is larger than the density of 20000 per m^2 found by Coe (1953), although he gives no standard error of the estimate.

DISCUSSION and CONCLUSIONS

An examination of the anatomy and behavior of *Donax gouldi* reveals that this species feeds on material suspended in the water and not on deposits. This is evidenced by the efficient straining mechanism on the inhalant siphon (Fig-ure 3), by the general absence of sand grains within the mantle cavity and by an examination of the stomach contents. A similar feeding habit was outlined for *D. denticulatus* (Linnaeus) by Wade (1964). These species feed differently than *D. vittatus* (Yonge, 1949), where there is no straining mechanism on the inhalant siphon, and the tentacular lobes are curled back, permitting suspended material along with some deposits to enter freely.

This evidence removes another species of the Tellinacea from the deposit-feeding ranks (see Pohlo, 1966, with regard to feeding in *Tagelus californianus*). Yonge (1949, p. 39) states that *Donax vittatus* feeds primarily on suspended material but later (p. 433) he states "Like all Tellinacea, these animals [referring to *Tagelus californianus*] are deposit feeders." Subsequent authors, for example, Stasek (1961), have been misled in the belief that deposit-feeding is universal within the Tellinacea.

Certain features of the morphology of *Donax gouldi* are associated with suspension-feeding, and are not generally found in the deposit-feeding Tellinacea. The animal

A

DEPOSIT FEEDING TELLINACEAN
small gills, outer demibranch
upturned, large palps, no
straining tentacles

↑

SUSPENSION FEEDING TELLINACEAN
large complete gills, small palps,
straining tentacles

↑

EULAMELLIBRANCHIA OR
FILIBRANCHIA ANCESTOR
large complete gills, small palps,
straining tentacles, suspension
feeder

B

SUSPENSION FEEDING TELLINACEAN
large complete gills, small palps,
straining tentacles

↑

DEPOSIT FEEDING TELLINACEAN
small gills, outer demibranch
upturned, large palps, no
straining tentacles

↑

EULAMELLIBRANCHIA OR
FILIBRANCHIA ANCESTOR
large complete gills, small palps,
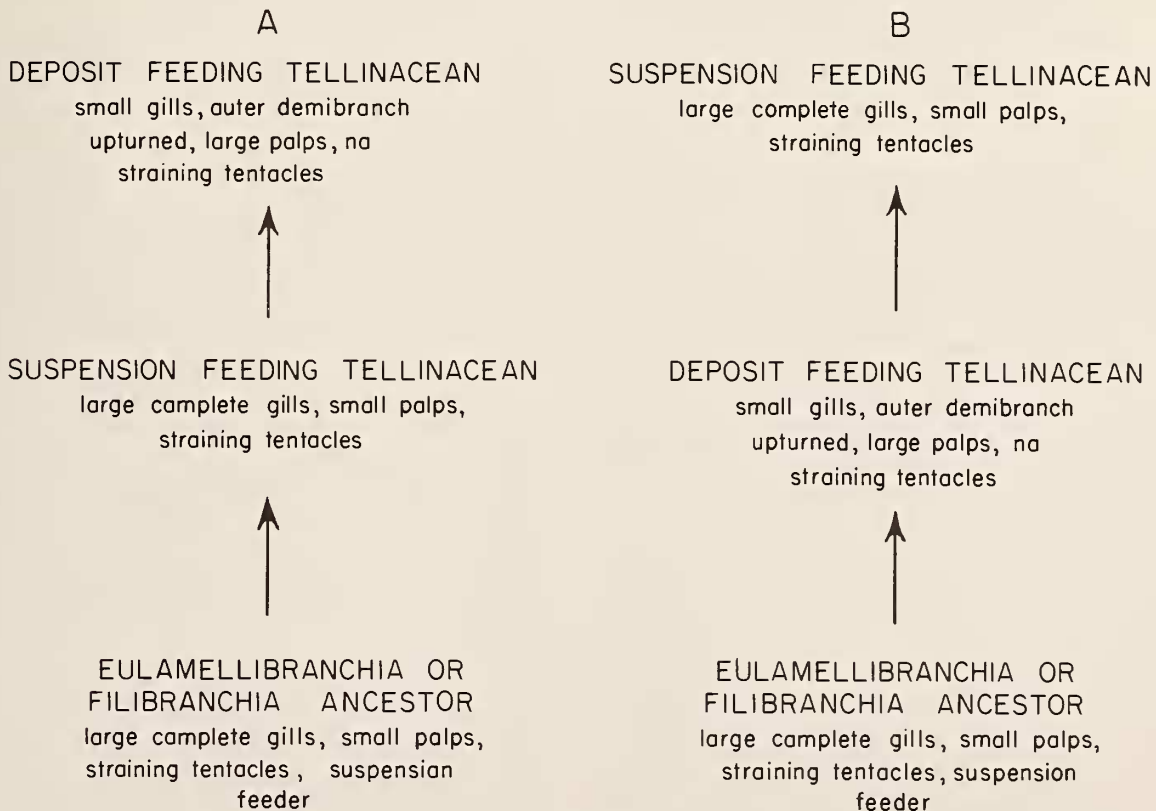straining tentacles, suspension
feeder

Figure 5
Two Possibilities for the Evolution of the Tellinacea.

has straining tentacles on the inhalant siphon. The ctenidia are complete, both demibranchs being large. In many Tellinacea the outer demibranch is upturned and reduced in size, a condition that prevents clogging (YONGE, 1949). Another feature of *D. gouldi* is that the ctenidia are large and the labial palps small. In deposit-feeding Tellinacea, such as *Macoma secta* (CONRAD, 1837) and *M. nasuta* (CONRAD, 1837) the opposite condition is true, and YONGE (*op. cit.*) states that this is correlated with the type of substratum. That is, where the deposits are firm the ctenidia are large and the palps small. The opposite condition occurs where the deposits are loose. This generalization does not appear to be true because *D. gouldi* is found on sand that is as loose as that found in the habitats of *M. secta*, and their gill and palp size-relationships are just the opposite from one another. It appears that in the case of *D. gouldi* the large gill and small palp is associated with suspension feeding.

The Tellinacea may have arisen from a suspension-feeding Filibranchia (YONGE, 1949, p. 72) or Eulamellibranchia stock (STASEK, 1963) and show progressive adaptations to deposit feeding. If this is so, a case can be made for *Donax* being an unspecialized or transitional type of tellinacean. An early tellinacean may have been a form with separate siphons bearing some straining device on the inhalant opening, two complete ctenidia, large gills and small palps, the approximate condition of some extant species of *Donax*. This type of organism would then give rise to a deposit-feeding tellinacean as shown in Figure 5A. It is difficult genetically to postulate that a suspension-feeding organism with two complete large ctenidia and probably with small palps gave rise to primitive Tellinacea that were deposit-feeders with upturned outer demibranchs and that lacked siphonal tentacles, and had large gills and small palps. This type of organism would then give rise to a suspension-feeding type such as *Donax* with two complete ctenidia, siphonal tentacles, large gills and small palps as shown in Figure 5B. This type of evolution necessitates that the morphology of a suspension-feeder was present in an ancestral tellinacean, then lost in the deposit-feeding Tellinacea, and then is regained in the suspension-feeding Tellinacea.

It is possible that *Donax* may possess certain neotenous characteristics as well as some primitive ones. A feature that could be equated with a primitive or neotenous condition is the stomach which is of Type IV, a condition that PURCHON (1960) regards as ancestral or simplified. In the other Tellinacea it is Type V, which is more advanced. Also, the gill and palp association of the Donacidae and Tellinidae is of Type III which STASEK (1963) interprets as neotenous.

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California Late Miocene Records of *Swiftopecten* HERTLEIN, 1935

(Pelecypoda : Pectinidae)

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(Plate 47)

UNTIL RECENTLY (STANTON, 1966), the lowest recorded West Coast occurrences of species of the pectinid genus *Swiftopecten* HERTLEIN, 1935, were from Middle to Upper Pliocene strata (ANDERSON, 1905; ARNOLD, 1906; NOMLAND, 1917; DALL, 1898, 1907). In fact, the genus was generally regarded as an index to the Pliocene (VEDDER, 1960, p. B 327).

As a result of detailed collecting in the Castaic Formation (Late Miocene) of Los Angeles County, California, STANTON (1966, p 27) discovered the oldest record of the genus, thus lowering the known range to the Late Miocene. Recently, while undertaking a detailed biostratigraphic study of the Neogene Formations of the Coalinga Region, California, the writer collected one almost complete specimen (Plate 47, Figures 1 and 2) and a fragment of the hinge area of another specimen belonging to this genus from the Late Miocene Santa Margarita Formation (Univ. Calif. Mus. Paleo. locality D-1088), exposed on Coalinga Anticline, about 9 miles north of Coalinga, California. These records unequivocally show that the genus *Swiftopecten* was already established along the Eastern Pacific during Late Miocene times.

The genus *Swiftopecten* probably evolved in the Western Pacific. The probable ancestral form, *Nanaochlamys kitamurai* (KOTAKA, 1955) (see MASUDA, 1962, p. 128) was common in Japan in beds as old as Late Oligocene. Younger forms representing successive stages of evolution, such as *Nanaochlamys notoensis* (YOKOYAMA, 1929) and *N. notoensis otutumiensis* (NOMURA & HATAI, 1937) (MASUDA, *loc. cit.*) also ranged to Middle or Late Miocene. The oldest Japanese record of the type species, *Swiftopecten swiftii* (BERNARDI, 1858) (the single survivor of the genus) is Middle Miocene (MASUDA, 1959; 1962, p. 196; UOZUMI, FUJIE & MATSUI, 1966). It, therefore, appears reasonable to assume that the western North American representatives of the genus were derived from Miocene immigrants from the Western Pacific.

STANTON (1966, *loc. cit.*) collected two fragmentary specimens from the Castaic Formation (Calif. Inst. of Tech. locality 1663). These were medium-sized, thin-shelled individuals, about 50 mm high. The sculpture, which was reflected internally, consisted of a few low, broad ribs and furrows on which other smaller, finer riblets were superposed. About 3 riblets were present on